

BIASES IN DIETS DETERMINED FROM PELLETS AND REMAINS: CORRECTION FACTORS FOR A MAMMAL AND BIRD-EATING RAPTOR

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ABSTRACT.—Numerous studies of predatory birds worldwide report dietary proportions based on analyses of large numbers of pellets or prey remains. Such analyses are often severely biased, hence strictly unquantifiable, because some prey remains are more conspicuous or persistent than others. We investigated this bias for the bird- and micromammal-eating African Marsh Harrier (*Circus ranivorus*), using an essentially independent measure of diet, observed prey deliveries to the nest. Comparisons of the frequency of occurrence showed that bird prey, particularly large wetland species, were over-represented almost threefold among remains. Micromammals were under-represented about 1.5-fold, while fish, frogs and eggs were marginally over-represented. Analyses using pellets were also biased but in the opposite direction to that of remains. We show that by combining pellets and prey remains (collected with equal effort), accurate estimates of overall diet can be achieved. This was verified using month by month comparisons of micromammals, in which proportions derived from pellets and remains never differed by more than 10% from those established from direct observations.

Parcialidad en los resultados para dietas determinadas por egagrópilas y residuos: factores de corrección para el caso de raptores que se alimentan de mamíferos y aves

EXTRACTO.—Numerosos estudios sobre aves de presa, en todo el mundo, informan sobre proporciones de dietas basadas en el análisis de un gran número de egagrópilas, o en el de residuos de presas. Tales análisis con frecuencia resultan muy parcializados, por tanto no cuantificables, debido a que algunos de los residuos de presa son más conspicuos o persistentes que otros. Hemos investigado esta parcialidad, para aves de rapiña de la especie *Circus ranivorus*, las que se alimentan de aves y mamíferos muy pequeños. Hemos usado una medida de dieta esencialmente independiente, tal como la observación del acarreo de presas al nido. Comparaciones de la frecuencia de ocurrencias mostró que las presas constituídas por aves, particularmente especies grandes de zonas pantanosas, fueron sobre-representadas por los residuos casi en el triple. Mamíferos muy pequeños fueron sub-representados en aproximadamente 1.5; mientras que peces, ranas y huevos fueron marginalmente sobre-representados. Los análisis que usaron egagrópilas han sido también parcializados pero en sentido opuesto al de los residuos. Demostramos que combinando egagrópilas y residuos de presa, colectadas con igual cuidado, estimaciones precisas de la dieta general pueden ser logradas. Esto ha sido verificado usando, mes a mes, comparaciones de dietas constituídas por mamíferos muy pequeños, en las que las proporciones derivadas de egagrópilas y de residuos nunca difieren en más de 10% de las establecidas por observación directa.

[Traducción de Eudoxio Paredes-Ruiz]

It is probable that the majority of predator studies rely on prey remains in some form to determine the diet of their subject. This is particularly so for wide-ranging or elusive birds such as raptors both in Africa (e.g., Steyn 1982, Tarboton and Allan 1984, Boshoff et al. 1990), Europe (Newton and Marquiss

1982, Korpimäki 1985) and North America (review by Marti 1987). Indeed, for one group, owls, there is rarely any other way of assessing diet but from pellets (Jaksić and Marti 1981). While most studies acknowledge that prey remains at nests or feeding sites may not be representative of what is actually taken (Newton and Marquiss 1982), quantitative estimates of the biases inherent in such analyses are almost non-existent for wild birds. Several studies have, however, attempted this by feeding captive

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birds known diets and subsequently identified what occurs in the pellets (Yalden and Yalden 1985, Village 1990). Alternatively, wild birds can be observed or photographed with time-lapse cameras for long periods at the nest to determine what is delivered; these data may then be compared with simultaneously collected remains and pellets to determine the biases (e.g., Jarvis et al. 1980, Collopy 1983, Marti 1987). The ultimate goal is to determine what an individual is eating using a correction factor for each type of prey category assessed.

Our purpose here is to quantify the biases inherent in dietary analyses based on remains and pellets alone. We examine the diet of an avian predator, the African Marsh Harrier (*Circus ranivorus*), which consumes both birds and mammals ranging in size from tiny mice of 7 g to game birds up to 700 g. Specifically, we ask: are birds over-represented in remains and if so by how much do large birds predominate over small birds, are micromammals under-represented and do some mice predominate over others? We subsequently show that by combining data from pellets and remains, an accurate assessment of diet can be achieved.

We use the term "micromammals" in preference to the more usual "small mammals" to emphasize that only the extreme lower mass range of mammals on the African continent were captured by the harriers studied. Furthermore, we are solely concerned with the frequency of occurrence of prey in the diet, not the biomass. The biomass consumed by an individual is itself strongly biased when computed from average prey weights as advocated by some (e.g., Craighead and Craighead 1956, Steenhof 1983). This arises because mammalian prey of lower than average mass may be taken more frequently than predicted (e.g., MacWhirter 1985), bird prey in harrier diets are typically juveniles (e.g., Barnard et al. 1987, this study) and smaller raptors rarely consume all of the prey they capture (leaving major bones), again biasing upwards the biomass estimates computed. Ways of avoiding or alleviating these biases in the laboratory (Wijnandts 1984), field (Masman 1986, Simmons 1986a) or via statistical procedures (Marti 1987), have been discussed elsewhere.

STUDY AREA AND METHODS

In a 3-year study of African Marsh Harriers on the southern coast of South Africa (34°00'S 22°40'E), we collected and identified remains at nests and known feeding sites regularly from about one month before breeding until the young became independent (6–7 mo each year, Sim-

mons 1989). Collections varied, however, and generally yielded little at the start of breeding, increased for nests at which adults were incubating or brooding, and decreased as large or flying young found and consumed all prey left by the adults. Remains were sorted to identify individuals and subsequently removed. Extensive data on delivery patterns and prey types were concurrently collected at 19 nests over a three-year period (Simmons 1989). These observations, totalling 2200 h, began about 1 mo before breeding each year and were continued throughout breeding for 6 mo. Nest watches were also evenly spaced over the daylight period and results presented here are based on 701 observed deliveries to nests observed from hides placed 60–100 m away.

As a third measure of diet composition, we simultaneously collected pellets from the same pairs. To both concentrate pellet collections and protect them from ubiquitous mammalian carnivores, we provided perch posts for territorial males, and once birds began to regularly use them, wound chicken-wire baskets around posts to catch all regurgitated material. The baskets were high enough and afforded sufficient protection to thwart mongooses that visited such areas. We do not claim that all pellets cast were collected, but birds preferred our posts to their previously used ground roosts, thereby allowing a larger than usual sample. Harrier pellets, notoriously difficult to analyze because few bones, only teeth and skull parts remain undigested, were analyzed using extensive museum reference material. We thus had three partly independent measures of diet: remains, pellets and direct nest observations. Direct observations are judged the best indicator of diet (Marti 1987) because they represent a delivery by delivery account of what breeding harriers brought to their nests, and they also represent the largest most uniform sample. Naturally, this method is itself not completely representative of what each bird catches; not all of the largest or smallest items may be brought to nests because of foraging constraints (Simmons 1986b), and small or partly dismembered items were not always identifiable in the grasp of flying birds. We do not believe these are serious biases, however, because large items (>200 g), those most likely to be missed because they are not carried to the nest, comprised only 3% of all 707 identified prey, and very small items were frequently delivered.

RESULTS

Diet from Direct Observations. Of 701 prey items delivered to 19 harrier nests between 1984 and 1986, 374 could be identified. Of these, 74% were micromammals (rats, mice and shrews), and 23% passerines and waterbirds. The remainder comprised small frogs (2%) and fish (1%). Considering only the micromammals (N = 326), 89 could be identified to species; 51% were *Rhabdomys pumilio*, and 43% *Otomys irroratus*. The remaining 6% were shrews (Table 1). Micromammals, therefore, predominated in the diet of these marsh harriers.

Bird Prey Biases in Remains and Pellets. Of 82 remains collected at harrier nests or feeding areas,

Table 1. A comparison of the diet of African Marsh Harriers determined from direct observations, pellets and prey remains.

PREY TYPE	DIRECT OBSER- VATIONS (374) ^a	PELLETS (251) ^b	REMAINS (82)
Micromammals	74%	83%	48%
<i>Rhabdomys</i>	51%	38%	47%
<i>Otomys</i>	43%	44%	39%
Shrews	6%	8%	11%
Birds	23%	14%	40%
Frogs	2%	0%	4%
Fish	1%	2%	5%
Eggs	0%	1%	4%

^a Number of items within each category.
^b Number of individuals identified from 156 pellets.

40% were birds. Observed deliveries and pellets both showed that considerably fewer birds occurred in the diet, than found in remains (Table 1). Thus, remains at harrier nests or plucking areas over-estimated bird prey 1.7-fold according to direct observations (the most accurate method) and 2.9-fold according to pellets.

In pellets, however, the frequency of individual birds was under-estimated according to direct observations. Only 14% of all prey identified in pellets were birds, whereas direct observations showed that birds comprised 23% of the diet, a 1.6-fold difference. Thus the two methods either over-estimated (remains) or under-estimated (pellets) the proportion of birds in the diet. Pellets were marginally more accurate.

Biases Among Bird Prey. Wetland birds which were commonly seen in the area but never found or

Table 3. A comparison of the seasonal proportions of micromammals derived from pellets and remains, relative to those from direct observations (N = sample size).

MONTH	PELLETS AND REMAINS (N)	DIRECT OBSERVATIONS (N)
July	85% (26)	75% (4)
August	88% (65)	80% (71)
September	77% (70)	84% (110)
October	70% (44)	66% (105)
November	60% (53)	67% (67)
December–January	51% (41)	53% (19)

identified in pellets, included coots (*Fulica* sp.), various rallidae and flufftails (*Sarothrura* sp.). Such prey were, however, present in prey remains, and comprised 30% of the 40% total birds (Table 2). Birds that could be identified in pellets were typically smaller species (doves, warblers and weavers). Hence, large avian species were more likely to be found in remains and smaller species in pellets. We could not quantify the bias because of the large number of unidentified avian prey in pellets.

According to remains, avian prey became prominent from October (67%) and predominated thereafter (Table 2). Since harriers partially switch to young avian prey as mouse abundance and vulnerability declines (Simmons 1989), this was not unexpected. However, according to direct observations, birds never exceeded small mammals in the diet of these harriers. Once again, therefore, birds were over-estimated in remains.

Micromammal Prey Biases in Remains and Pellets. Of the 82 prey remains only 48% were micromammals—mainly *Rhabdomys pumilio* (46%)

Table 2. Summary of monthly differences in Harrier prey composition assessed from remains found at nests and plucking sites, 1984–1986.

	MICRO- MAMMALS	BIRDS	FROGS/FISH	EGGS	PROPORTION OF MAMMALS : BIRDS
July–August	16	2	2	0	79%:11%
September	12	6	2	2	57%:26%
October	3	10 [2] ^a	1	1	20%:67%
November	7	8 [4]	1	0	44%:50%
December–January	0	7 [1]	1	0	0%:88%
Totals	39	33 [7]	7	3	48%:40%

^a No. of juveniles in the total.

and *Otomys irroratus* (38%). Since micromammals comprised 73% of the diet from direct observations (Table 1), remains under-estimated this prey type 1.5-fold. However, for the two main species of micromammals, *Rhabdomys* and *Otomys*, the relative difference in their proportions (8%) was identical from both methods.

Pellets appeared to be the least accurate method of assessing which micromammals occurred most often in the diet, since our analyses suggested that more *Otomys* than *Rhabdomys* were eaten by harriers. By providing certain harriers with supplementary food (Simmons 1989), we could determine one reason why the large (50–200 g) *Otomys* were more likely to be found in pellets than the 30–80 g *Rhabdomys*; *Rhabdomys* were typically completely eaten except for a small section of the skull, including the jaw, which was often discarded. This was not so for *Otomys*. Hence the skeletal elements that provided the most reliable means of identifying this species would not always appear in the pellet. Under-representation of *Rhabdomys* in pellets was thus explicable.

Greater Musk Shrews (*Crocidura flavescens*), strongly scented 30 g insectivores, were observed being caught but discarded by African Marsh Harriers, presumably because of their strong musk and taste (cf. Smithers 1983). For example, in one case a complete specimen lay untouched at an active feeding site for 4 days. According to remains they should, therefore, be over-represented in the diet. This was so (Table 1), but samples are very small.

Other Prey Types. In general, other prey taken by harriers were more likely to be found in remains than either pellets or direct observation. Hence frogs and eggs were apparent in remains but were rarely recorded in pellets. The value of studying remains, therefore, lies in exposing the more unusual items rarely recorded by other methods.

Correcting Biases: Pellets and Remains Combined. When diet composition from prey remains and pellets were combined ($N = 333$), the proportion of micromammals in the diet (74%) was exactly that recorded from direct observations. Similarly, proportions of bird prey from pellets and remains (20%) were nearly identical to that found from direct observation (23%). Hence it seems that for harriers, remains and pellets can be combined to increase the accuracy of prey analyses. Similar conclusions were reached by Collopy (1983) studying Golden Eagles (*Aquila chrysaetos*).

As an additional check on the accuracy of this

possible correction factor we undertook a seasonal assessment, combining remains and pellets by month. Again, the correspondence between proportions of micromammals derived from remains and pellets were almost identical to that found by direct observation (Table 3). In any one month, the proportion of dietary micromammals found by pellets and remains, did not differ by more than 10% from that found by direct observations. The differences ranged from 2–10% (for the lowest sample size) and averaged 6.3%—a difference small enough to be explained by chance.

DISCUSSION

This study quantifies what many avian researchers have often suspected—that birds are seriously over-represented in the prey remains of mammal/bird-eating raptors. This is the first study, however, which attempts to both quantify and subsequently rectify such biases for a free-ranging raptor taking micromammals. That bird prey can be over-estimated almost threefold was unexpected, and shows the value in expending considerable time in determining diet from direct observation. Since avian researchers seldom have the time or perhaps the inclination to sit for hundreds of hours watching their quarry, we have provided a much simpler method of determining dietary intake. By combining pellets and prey remains we show that for any one month, proportions of micromammals differ by an average of 6% (and no more than 10%) from that actually observed. This considerable time-saving finding may also allow much greater accuracy for diet determination of raptors that are known (or suspected) to switch prey at certain seasons. That the method of combining pellets and remains gives accurate estimates for harriers (this study) and eagles (Collopy 1983), suggests that it may have a more universal application for mammal/bird-eating raptors than presently appreciated.

For these methods to be applicable in other studies it is necessary to determine the number of pellets and prey remains required, and in what proportions, for an accurate assessment of diet. In this study, we collected remains and pellets with equal effort on an approximately monthly basis. That pellets outnumbered remains (about twofold) was a natural phenomenon attributable to the harriers and not to any differential collecting effort. We also took care to increase our efficiency in pellet collecting, by providing perch posts within the territories of each har-

rier, thereby minimizing the numerous possible areas in which birds might cast pellets. As previously stated, these collections were also protected against ubiquitous mammalian predators.

In conclusion, it seems that the value of studying diet from direct observations lies in the consistency and accuracy of such a method. On the other hand, studying pellets allows a more accurate assessment of species composition, particularly small micro-mammals seldom recorded by direct observation. Lastly, the value of studying remains, while biasing the more common remains in favor of birds, allows us to determine more unusual prey such as eggs and fish. Each method, therefore, has its advantages. The most important point, however, is that it is possible, at least for harriers, to circumvent biases inherent in collecting just remains or pellets by combining them. Dietary proportions within about 10% of the "true" diet are then possible.

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